

## **Response Of Soil Collembola (Insecta) Communities To Forest Disturbance In Central Amazonia (Brazil)**

**Oliveira E.P. and Deharveng L.**

UPR 9014 du CNRS, Laboratoire de Zoologie

Université P.Sabatier, 31062 Toulouse-Cedex (FRANCE).

### **RESUME**

Les Collembolles du sol ont été prélevés chaque mois pendant 14 mois dans une forêt primaire et une forêt secondaire de 6 ans près de Manaus (Amazonie Centrale, Brésil). Des différences importantes dans la structure des peuplements ont été observées entre les deux types de forêts. Sur un total de 75 espèces de Collembolles (pour 6050 individus récoltés), 14 étaient absentes de la forêt secondaire et 7 de la forêt primaire. La structure du peuplement montre une dominance plus forte de l'espèce la plus abondante dans la forêt secondaire, ainsi que du contingent des espèces généralistes - parthénogénétiques-pantropicales; parallèlement, équitabilité et abondance sont plus faibles globalement et pour la plupart des dates de récolte. Les différents indices de diversité présentent des fluctuations plus importantes dans la forêt secondaire, où une évolution saisonnière est perceptible en relation avec un sol plus exposé aux variations microclimatiques. Six ans après la perturbation, le peuplement de Collembolles reste encore fortement appauvri par rapport à celui de la forêt primaire, malgré une vigoureuse régénération forestière et des conditions écologiques favorables à la recolonisation par la faune édaphique.

## ABSTRACT

Soil Collembola communities have been sampled every month over 14 months in a primary and a 6-year old secondary forest of Central Amazonia. Important differences in the structure of Collembola communities were observed between the two forest types. Within a total of 75 Collembola species (for 6050 specimens), 14 were absent from secondary forest and 7 absent from primary forest. Community structure is characterized by a higher dominance of the most abundant species, and of the generalist-parthenogenetic-pantropical element of the fauna in secondary forest; parallelly, evenness and global species abundances are lower in secondary forest, for the complete set of samples as well as for most of the sampling dates. The different diversity indices fluctuate more in secondary forest where soils are more exposed to climatic variations, with some indications of seasonal changes in the communities. Six years after site disturbance, soil Collembola communities had therefore not yet recovered in spite of intense regeneration and favourable conditions for recolonization.

**Keywords:** Amazonia, soil fauna, Collembola, community ecology, deforestation, primary rainforest, secondary rainforest.

## Introduction

Arthropods represent by far the major component of biological diversity in tropical forest soils. Yet, little is known about their community organization and dynamics, in spite of the increasing concern about deforestation and loss of biodiversity which recently emerged among ecologists. In Amazonia, the largest block of primary forest on the planet, several authors have analyzed the soil communities of microarthropods at the level of taxonomic groups (Betsch 1987, Dantas 1978, Hüther 1983, Melo 1985, Teixeira & Schubart 1986, Adis & Schubart 1989). In contrast, two papers only addressed the problem at a specific level, a much more informative (Usher 1988) but more difficult and time-consuming approach: Oliveira (1983) for epigeic Collembola and Ribeiro (1986) for Oribatida. Edaphic Collembola, the second arthropod group in soils in terms of diversity and density (after Oribatida), are considered here for the first time from that point of view. The aim of the present work is to evaluate (1) what is the overall response of rainforest Collembola communities to site disturbance, (2) at what extent Collembola communities

exhibit seasonal patterns of diversity, and (3) how these patterns are altered by forest disturbance. For this purpose, we compared soil Collembola in a plot of secondary forest and in an adjoining block of primary forest along a complete annual cycle. This study was part of the multidisciplinary project "Bacia Modelo" developed by INPA from 1979 to 1983.

## Material and methods

Study sites are located on a plateau 80 km north of Manaus in Central Amazonia (Brazil, lat. 02°34'S, long. 60°06'W, Fig.1). Soils of the area, defined as yellow latosol, contain about 80% of clay (Chauvel 1981). The secondary forest site had regenerated after complete logging and prescribed burning of 9 hectares of rainforest in 1976. The primary forest site is located about 4 km far, with the same soil and slope conditions. Both sites were sampled 14 times between April 1981 and June 1982, including a full dry season (June to November) and a full rainy season (December to May) (Ribeiro & Adis 1984). Ten samples of 25 cm<sup>2</sup> down to 3 cm depth were analyzed in each site at each sampling date. Temperature was measured at 5 cm depth and soil water content was measured at 5 points with the same frequency. Fauna were extracted with a Berlese-Tullgren apparatus and

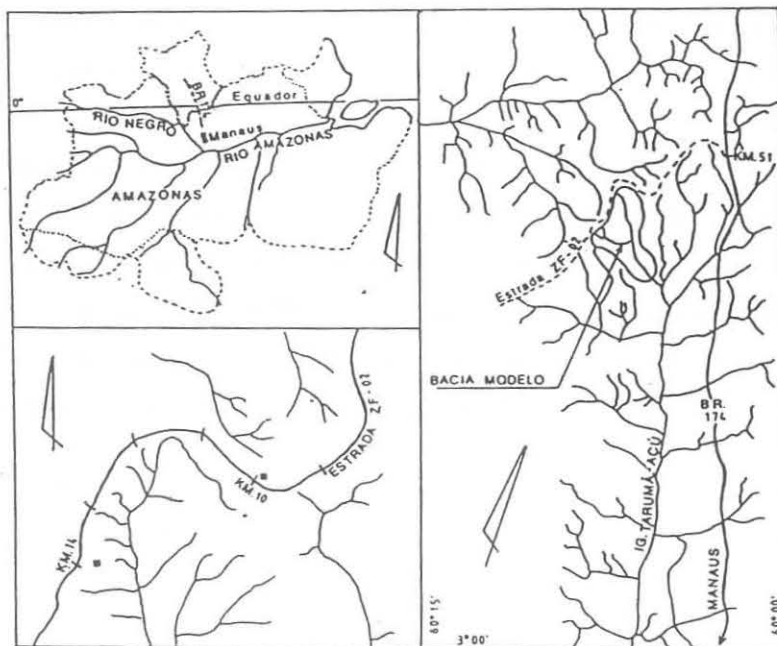


Figure 1 - Localization of the study sites.

sorted at the INPA (Manaus). Identifications were made at the University of Toulouse (France).

Diversity has been measured by the following indices (Magurran 1988):

Species richness (S): number of species in the sample;

Berger-Parker index (B.P.): relative abundance of the most abundant species in the sample;

Shannon evenness:  $E = H' / \log_2(S)$  where  $H'$  (Shannon index) =  $-\sum(p_i \cdot \log_2(p_i))$ ,  $p_i$  = relative abundance of the  $i$ th species.

## Results

Collembola abundance (Fig. 2, Tab.1) - A total of 6050 specimens of Collembola were extracted from the 280 soil samples: 3428 specimens from 140 samples in primary forest, 2622 specimens from 140 samples in secondary forest. The abundance of Collembola in secondary forest compared to primary forest is lower in 10 out of the 14 sampling dates. No clear seasonal trend was observed and soil humidity was not correlated with abundance in either forest site.

Species richness (Fig. 3, Tab.1) - On the whole, 75 species were present in our material. This number is however an underestimate of the real species richness, as three genera (*Lepidocyrtus*, *Lepidosira* and *Sphaeridia*) and two families (Dicrytomidae and Neelidae) have not been resolved at the species level because of taxonomic uncertainty. A total richness of 85-90 species would be a reasonable estimate, given the relatively low diversification of these taxa in our samples. The number of species was constantly lower in secondary forest than in primary forest, except for October 1981, with an overall difference of 7 species for the complete set of samples. As for abundance, no clear seasonal trend was observed.

Species dominance (Fig.4, Tab.2) - In all sampling periods except August 1981, the Berger-Parker index is higher in secondary forest than in primary forest. A seasonal trend appears for secondary forest, with B.P. increasing during the dry season. In contrast, no correlation was found between soil water content and B.P. in primary forest. In this last site, the variations of B.P. were much lower (0,10 to 0,20) than in secondary forest (0,12 to 0,44), a difference which parallels the much lower variations in soil humidity.

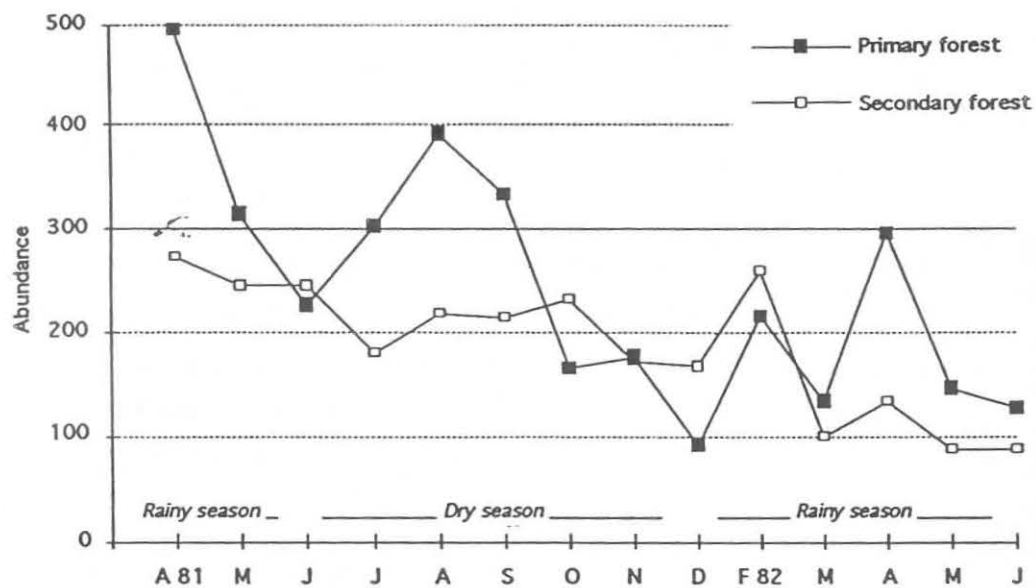


Figure 2 - Monthly evolution of Collembola abundance.

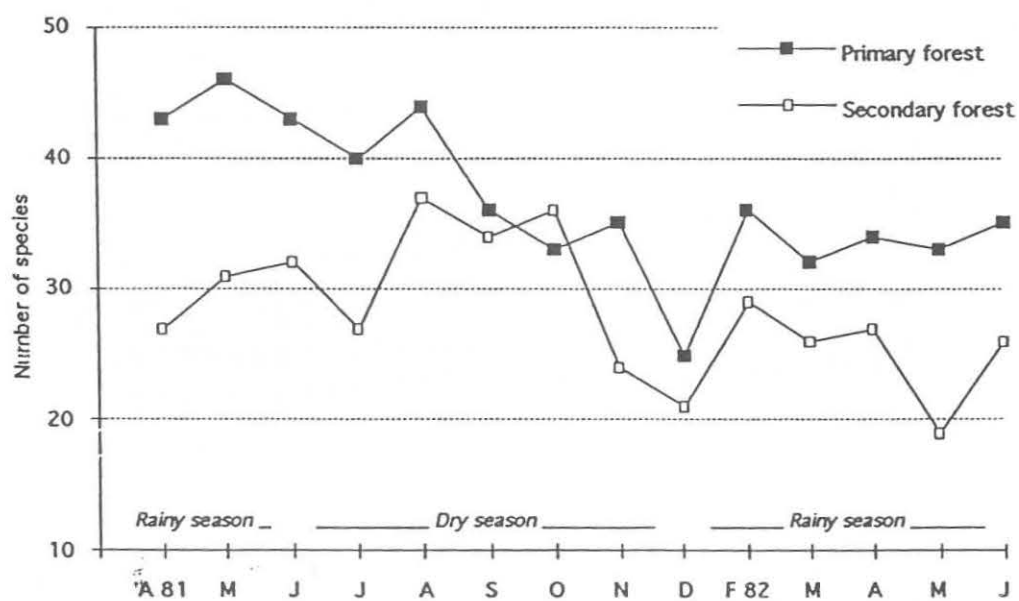


Figure 3 - Monthly evolution of Collembola species richness.

	Primary forest													Ab	Oc	Secondary forest													Ab	Oc			
	1981												1982																				
	A	M	J	J	A	S	O	N	D	F	M	A	M			J	A	M	J	A	S	O	N	D	F	M	A	M			J		
<i>Aethiopella</i> sp	1		1								1	2	1		6	5				3		1		1			1	2		9	6		
<i>Arhopaetes</i> sp	37	12	17	20	10	12	8	9	5	20	11	19	16	9	205	14		1	3		2				1	4	2	2		15	7		
<i>Brachyromella</i> sp1	4	8	2	1	2	1	2	1		2					23	9		1	8	2	2	1		1		1	2	5		23	9		
<i>Brachyromella</i> sp2	1	4										1			6	3		2	2				1		2		1	1	2	1	12	8	
<i>Brachyromellides compitus</i> Arlé 1999	3	4	2							1		2	1		13	6																	
<i>Campylorhynchus schaefferi</i> Boemer 1905		3			2			1			1	1	1	2	11	7										1				2	2		
<i>Celophora</i> sp			1												1	1			1												1	1	
<i>Cryptopygus</i> sp	3	3	2	6	4	3	4	1	2		2	2	2		34	12		1		4			2	2			1		3	13	6		
<i>Cyphodirus</i> sp1	2	6	6	2	3	2		7	1	1	1	3	5		39	12		9	4	5	5	4	3	2	4	2	9	5	5	4	61	13	
<i>Cyphodirus</i> sp2	1	2	1		1							1	3		9	6		1		6	2		1						2		12	5	
<i>Dicranocentrus</i> sp	4	2	1	2	2	2	1	1				2	3	3	23	11					1										1	1	
<i>Dicranomys</i> sp		2	3	2	2	2				1		3	3		18	8		2	1	2		1	1	2							9	6	
<i>Entomobrya eglei</i> Arlé & Guimarães 1978				1		1	1								3	3																	
<i>Entomobrya</i> sp	2	1		1	2	1		2	2			7	2		20	9		2			3							2		7	3		
<i>Entomobrya uambae</i> Arlé 1999		2		1	2	1									6	4																	
<i>Folsomides americanus</i> Denis 1931										1					2	2			6	1	3	4	13		1	4		2	12		46	9	
<i>Folsomides centrali</i> (Denis 1931)		1																8	1	11	4	3	3	2	4	5					41	9	
<i>Folsomia anyakulina</i> Denis 1931	82	31	18	16	34	44	14	21	3	9	9	7	1	6	295	14		27	19	12	20	24	35	31	51	75	69	12	6	4	3	388	14
<i>Furculanurida</i> sp1		2			1										3	2																	
<i>Furculanurida</i> sp3	3	1	2	3		1	1	3	2	3		2	1	2	24	12			5				1		2			1	4	14	6		
<i>Guyanocryptus</i> sp														1	1	1																	
<i>Isoptomella amazonica</i> Oliveira & Deharveng 1990										1					1	1				3											3	1	
<i>Isoptomella arlei</i> Oliveira & Deharveng 1990	21	10	1	5	9	2	2	2	1	1	2	8	1	2	67	14		6	8	3	2	4	7	7	1	1		1	2	1	43	12	
<i>Isoptomella basai</i> Deharveng & Oliveira 1990										1		1			2	2		1	2											1	5	4	
<i>Isoptomella digitata</i> Deharveng & Oliveira 1990																				3											3	1	
<i>Isoptomella duplicata</i> Deharveng & Oliveira 1990	8		5	1	5	8	1	1	1	3	2	6	1	2	44	13																	
<i>Isoptomella granulata</i> Oliveira & Deharveng 1990	12	5	7	15	11	19	3	8	1	12	9	9	1		112	13		11		5	6	1	1		1	2	1	1		29	9		
<i>Isoptomella hummilleri</i> Deharveng & Oliveira 1990	71	29	31	31	47	47	27	18	8	19	14	42	7	12	403	14		62	63	61	42	24	14	24	3	4	43	18	19	33	16	426	14
<i>Isoptomella quadricolor</i> Deharveng & Oliveira 1990																																	
<i>Isoptomella sensillata</i> Oliveira & Deharveng 1990	9		2		3	13	1	4		2	3	7	1		45	10													2		3	2	
<i>Isoptomella similis</i> Oliveira & Deharveng 1990	6	3	1	1	10	6	1	1			1	2	1		33	11		1	8	5	5	5	8	8	4	9	5	8	2	1	2	71	14
<i>Isoptomella spinifer</i> Deharveng & Oliveira 1990	11	2		4	6	2	4	3	1	3	3	3	1	1	44	13																	
<i>Isoptomella symmetrisulcata</i> Hagi & Thibaud 1987	25	35	26	33	77	30	23	22	12	42	19	20	11	20	395	14		34	28	30	28	33	25	44	19	16	29	10	16	18	7	337	14
<i>Isoptomella thibaudi</i> Denis 1923	13	11	8	3	10	10	5	7	6						73	9		11	12	5	7	12	22	18	21	8	2	2	10		130	12	
<i>Isoptomys</i> sp															1	1				3	1	3	1	1		1	1			1	12	8	
<i>Lepidocyrtus</i> sp	3	9	1	2	4	3	1	4	1	2	1	2	4	2	39	14		2			2	4	5	1	3	4		1	2	1	25	10	
<i>Lepidocyrtus</i> sp	1	1	1	2	2						1	1	2		11	8			1	1		1		1		2	2			1	9	7	
<i>Metopocera</i> sp		4	1	1											6	3		2			1	3	1	1	1		1		1	1	12	9	
<i>Metopocera campani</i> Handshien 1934																																	
<i>Metaphorura amazonica</i> Oliveira & Thibaud 1992	8	4	2	6	6		1			1	2	4	1	1	36	11		4		1									7		13	4	

<i>Metaphorura</i> yosi Rusek 1967	1	1	1				1								6	6	5	31	5	10	14	20	30	26	20	12	2	3	1	3	182	14	
<i>Neelidae</i> spp.	60	12	8	36	14	22	4	7	9	17	5	30	14	2	240	14	19	8	18	5	8	8	2	1	3	13	5	11	3	2	106	14	
<i>Neotropilella</i> arlei Nagl, Thibaud & Weiner 1990	4			3								1	4		12	4				2											3	2	
<i>Neotropilella</i> carli (Denn 1934)																										2					2	1	
<i>Neotropilella</i> digrammaronata Thibaud & Massoud 1963	2	2	5	1	4	6	4	1	1		7	3	1	3	40	13	1	1	1	4	3	4	1		3	5	2		5	30	11		
<i>Neotropilella</i> meridionalis (Ahlé 1939)		1	1					1	2					1	2	8	6																
<i>Neotropilella</i> sp1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	10	9			6	2	4	4			1	5	3	2	1	1	29	10	
<i>Neotropilella</i> sp2		1			1										2	2																	
<i>Neotropilella</i> sp3					2										2	1																	
<i>Neotropilella</i> vanderdriem (Massoud 1963)	2		1	2	1	1	1	5							13	7	10	4	3	2	1	1	2	3		6		6	4		42	11	
<i>Paranura</i> nuda Castagnau & Oliveira 1990	6					2					2		1		11	4			2												3	2	
<i>Paranura</i> infima Ahlé 1959						1									1	1			1	1											1	4	
<i>Paranuraphys</i> sp1	3	10	1	2	8	3	1	1	3	3	1	10	4	3	53	14		4		3	1					1					10	5	
<i>Paranuraphys</i> sp2		1		3		3		1		1	2	2	7	1	21	9						2										3	2
<i>Paranuraphys</i> sp3			6		5										11	2																	
<i>Paronella</i> sp02	7	10	6	20	12	19	15	10	17	5	3	10	4	1	139	14	5		3	5	2	3	11	6		1	3	3			42	10	
<i>Paronella</i> sp05	1	4	1		3			1	1				1	1	13	8					2	2	2			1	4	2		1	1	15	8
<i>Paronella</i> sp08								1	2						3	2																	
<i>Paronella</i> sp11																																	
<i>Paronella</i> sp12		2													2	1							6									9	4
<i>Paronella</i> sp13	11	19	10	8	9	3			2	12	7	25	18	17	141	12	9	2	11	5	6	3	4			15	6	1	4	10	76	12	
<i>Paronella</i> sp01		3	1	1	1		2	1	2	1	2	2	2	1	19	12			2		1	1	1								1	6	5
<i>Prisotoma</i> sp	1														1	1																	
<i>Prisotoma</i> amazonica Castagnau & Oliveira 1990																	6		3	1	1							2			14	6	
<i>Pseudacharutes</i> cf. herberti Ahlé & Ruffa 1976		1	2												4	3																	
<i>Pseudacharutes</i> sp1	2	2		1	1										8	6																	
<i>Pseudacharutes</i> sp2	4		3	10			1	4	4	2	2	1			31	9		1	1							3					8	6	
<i>Pseudacharutes</i> sp3		3	2		2										9	5																2	2
<i>Pseudosinella</i> sp	7	5	7	7	5	17	4	13	2	5	4	8	5	2	91	14	3	1	1		4	1	2	1						3	17	9	
<i>Salina</i> cf. celebensis (Schaeffer 1898)			1	1											2	2																	
<i>Sphaerida</i> spp	8		2	5	1	3	2	1	1	1	2	2	1	3	32	13					1										2	3	2
<i>Sphyrrothea</i> sp1	1	10	10	2	11	5	3			7	3	24	12	4	92	12	7	5	5		3	1	3	3		2	1	2	4	36	11		
<i>Symphyleona</i> sp7							1								2	2						1											
<i>Trigolaphys</i> sp	9	5	7	9	6	8		5		4	1	6	2	1	63	12	4	3	3	2	5	3	1	2	2	2	1	4			32	12	
<i>Xenylla</i> sp																	1																
<i>Yosiella</i> miva Huether 1967	1			5		2									8	3							1										
<i>Isotomella</i> graminis Ind.	23	19	11	20	48	20	16	6	4	19	6	14	5	3	214	14	16	13	15	8	19	17	10	7	5	16	3	11	3	9	152	14	
<i>Olympiella</i> Ind.	12	2	3	9	1	8	8		1	6	3	5	8	4	70	13	8		1	1	3		1									14	5
Number of specimens	497	316	226	304	393	334	166	177	94	215	134	296	147	129	3428		275	244	244	180	218	214	232	173	168	259	101	135	89	90	2622		
Number of species	43	46	43	40	44	36	33	35	25	36	32	34	33	35	68		27	31	32	27	37	34	36	24	21	29	26	27	19	26	61		

Table 1. Collembola abundance; Ab: total number of specimens per species; Oc: total number of occurrences.

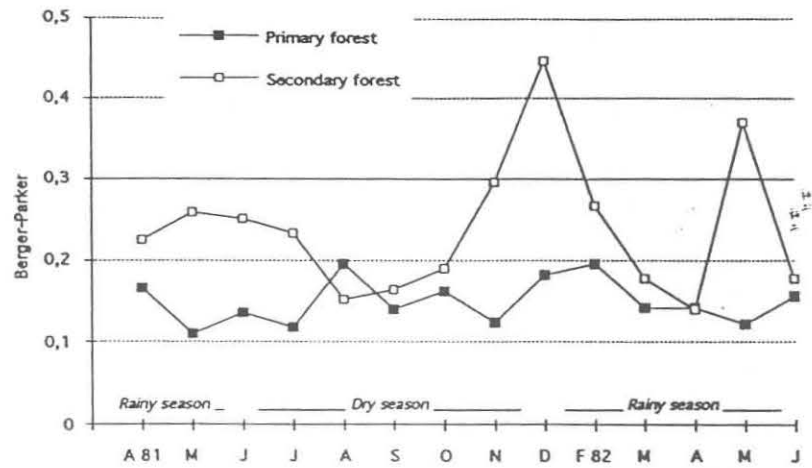


Figure 4 - Monthly evolution of Berger Parker index.

Primary forest		Number of species	Abundance	Shannon index	Evenness	Berger Parker	Soil humidity	Temperature -5cm	Precipitations
1981	A	43	497	4,21	0,78	0,16	52,51	25	211,8
	M	46	316	4,77	0,86	0,11	55,66	25	?
	J	43	226	4,54	0,84	0,14	52,38	?	162,3
	J	40	304	4,41	0,83	0,12	53,84	24,9	51,3
	A	44	393	4,34	0,79	0,20	46,78	24,6	176,7
	S	36	334	4,22	0,82	0,14	50,92	24,9	186
	O	33	166	4,07	0,81	0,16	45,43	26	72,2
	N	35	177	4,37	0,85	0,12	40,24	26,4	176
	D	25	94	3,99	0,86	0,18	51,41	24,4	230
	F	36	215	4,11	0,79	0,20	54,48	25,4	206,8
	M	32	134	4,37	0,87	0,14	58,05	25,2	242,2
1982	A	34	296	4,33	0,85	0,14	53,99	24,4	458,8
	M	33	147	4,31	0,85	0,12	57,56	26	252,4
	J	35	129	4,40	0,86	0,16	56,53	25,40	76,70
	Mean	36,79	244,86	4,32	0,83	0,15	52,13	25,20	192,55
Standard deviation		5,75	115,94	0,20	0,03	0,03	5,00	0,63	103,38

Secondary forest		Number of species	Abundance	Shannon index	Evenness	Berger Parker	Soil humidity	Temperature -5cm	Precipitations
1981	A	27	275	3,83	0,81	0,23	49,28	25	211,8
	M	31	244	3,77	0,76	0,26	57,2	26,2	?
	J	32	244	4,02	0,80	0,25	55,2	25,7	162,3
	J	27	180	3,83	0,81	0,23	43,56	24,3	51,3
	A	37	218	4,37	0,84	0,15	47,7	25	176,7
	S	34	214	4,07	0,80	0,16	44,28	24,8	186
	O	36	232	3,92	0,76	0,19	45,64	26	72,2
	N	24	173	3,38	0,74	0,29	42,69	26	176
	D	21	168	2,94	0,67	0,45	71,46	24,2	230
	F	29	259	3,58	0,74	0,27	58,35	24	206,8
	M	26	101	4,07	0,87	0,18	51,26	25,1	242,2
1982	A	27	135	4,12	0,87	0,14	52,68	27	458,8
	M	19	89	3,08	0,73	0,37	74,74	26,2	252,4
	J	26	90	4,12	0,88	0,18	47,81	24,40	76,70
	Mean	28,29	187,29	3,79	0,79	0,24	52,99	25,28	192,55
Standard deviation		5,28	63,77	0,41	0,06	0,09	9,85	0,91	103,38

Table 2. Diversity and microclimatic measures of Collembola communities in primary and secondary forest.



Shannon evenness (Fig.5, Tab.2) - Evenness is higher in primary forest in ten out of fourteen sampling dates. As for Berger-Parker index, the relative stability of evenness in primary forest contrasts with its large variations in secondary forest. Seasonal influence, unclear for primary forest, is well marked for secondary forest, with a decrease in dry season.

Generalist species (Fig.6, Tab.1) - Figure 6 gives the relative numerical importance in the communities of the pantropical-parthenogenetic element, which comprises a total of 7 species: six Isotomidae (*Folsomides americanus*, *F. centralis*, *Isotomiella nummulifer*, *I. symetrimucronata*, *Isotomodes trisetosus*, and *Folsomina onychiurina*) and one Onychiuridae (*Mesaphorura yosii*). These generalist species are largely dominant in the studied habitats for all sampling dates. Their relative abundance is higher in secondary forest, with only one (*I. symetrimucronata*) being less numerous than in primary forest. No correlation was found with habitat parameters or season in primary forest, but generalists increase in number during dry season in secondary forest. Surprisingly, the relative number of generalists changes in an opposite direction from month to month in primary and secondary forest.

Exclusive species (Tab.1) - Twenty-one (28 %) out of the 75 species present in the studied soil communities are not shared by primary and secondary forest. The former harbours 14 exclusive species against 7 in secondary forest. The numbers are respectively 10 and 2 when rare species (present in only 1 sample) are discarded. In addition, 35 species are less abundant in secondary than in primary forest, while only 19 are more abundant.

Major differences between communities of Collembola in primary *versus* secondary forest are finally summarized by box-plots of fig.7.

## Discussion

1) Global loss in biodiversity. Although literature and theoretical considerations suggest that early stages of moderate disturbance may lead to a temporary increase in biodiversity (Connell, 1978), no data supporting this view has ever been published for Collembola. All available studies indicate only that disturbed forest soils have a reduced diversity of Collembola compared to undisturbed or less disturbed ones (Bonnet et al 1979, Gers & Izarra 1983, Jordana et al 1987, Gama et al 1991). A similar trend was observed in our Amazonian site: all descriptors of community structure considered (species richness,

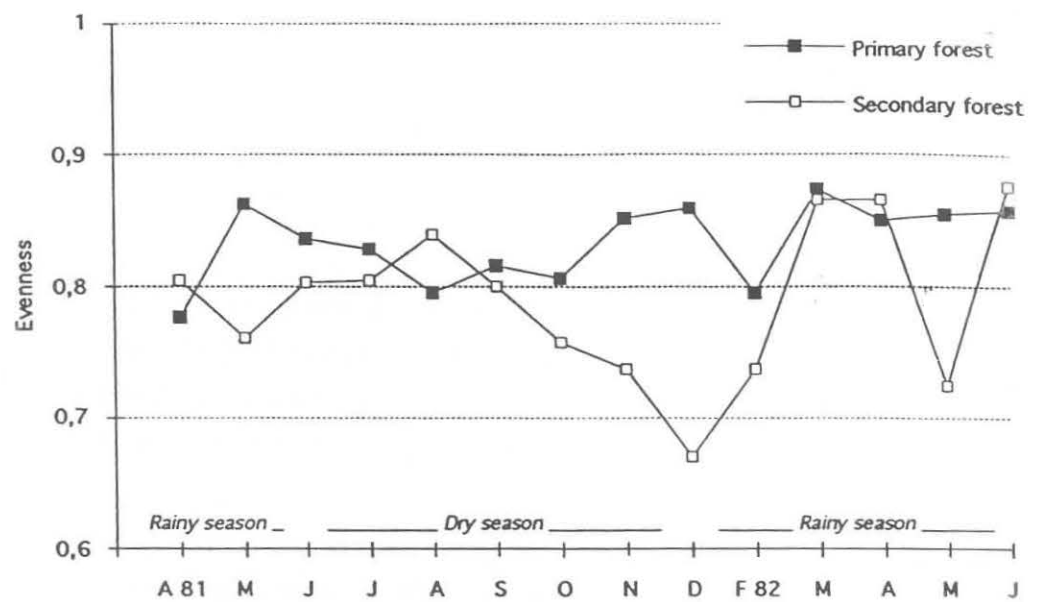


Figure 5 - Monthly evolution of Evenness.

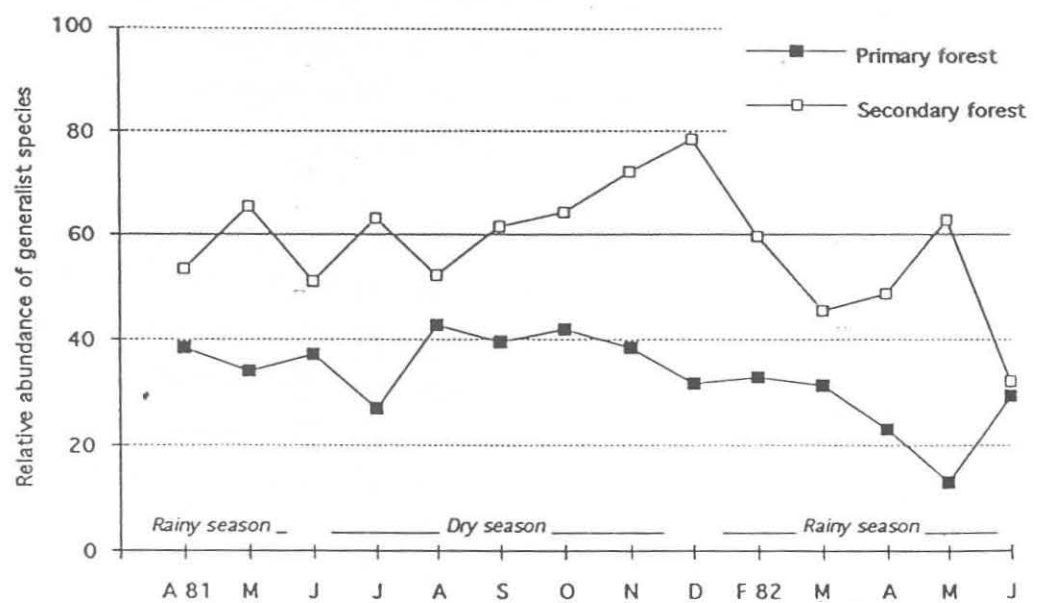


Figure 6 - Monthly evolution of the importance of generalist species.

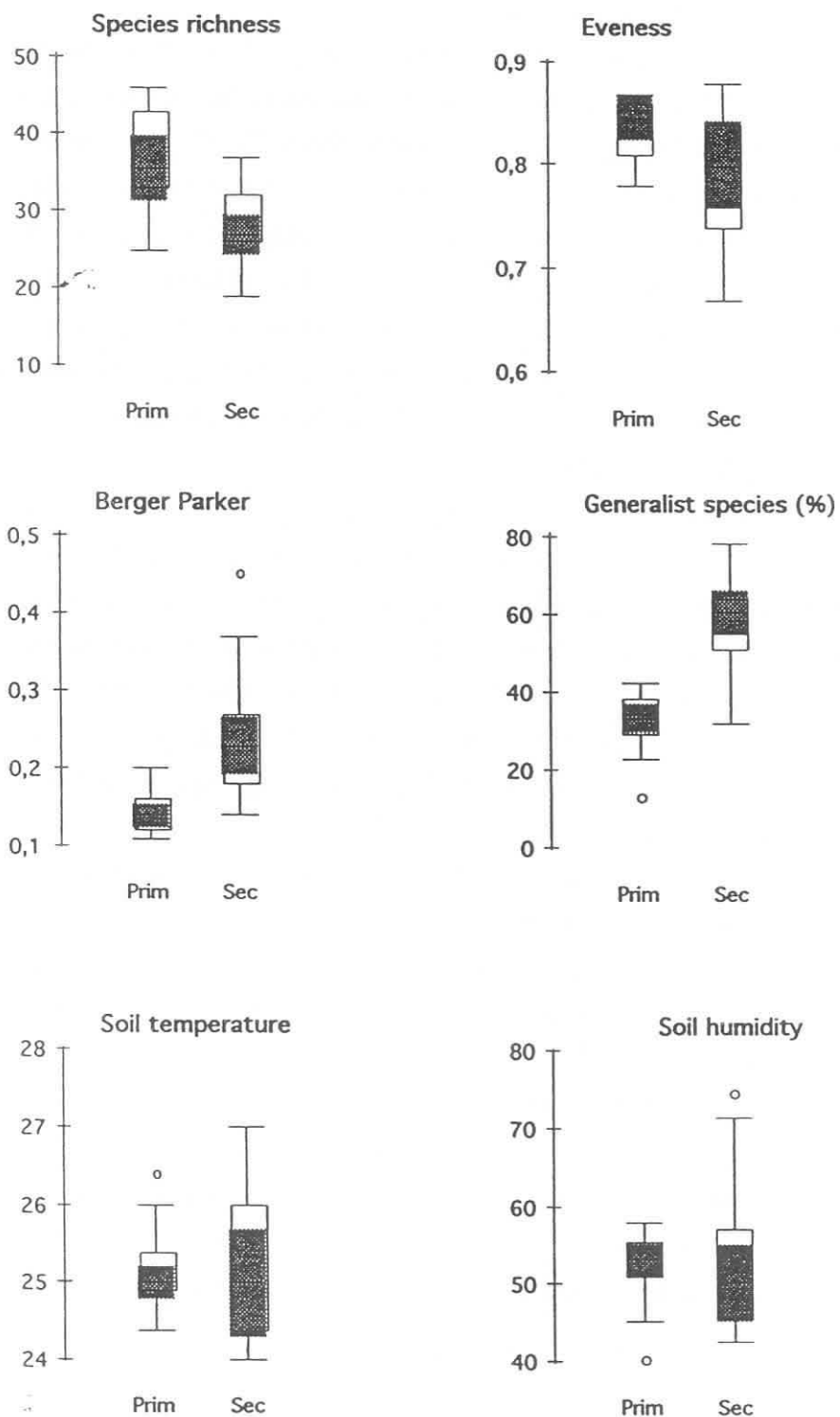


Figure 7 - Differences between primary and secondary forest illustrated by box plots of different parameter of community structure, soil temperature and soil humidity for the 14 months of the study.

evenness, Berger-Parker, relative number of generalists) indicate a lower biodiversity in secondary *versus* primary forest. These results are in agreement with those of Oliveira 1983 for epigeic Collembola of the same area, and those of Takeda 1981 for soil Collembola of Northern Thailand. In this last region, decrease in Collembola diversity was stronger and more seasonal, probably as a consequence of the more severe level of disturbance caused by cropping, and the more drastic dry season.

Authors working at higher taxonomic levels in Amazonia observed that the main groups of the soil fauna had reappeared a few years after rainforest disturbance (Betsch 1987, Betsch et al 1990, Silva del Pozo & Blandin 1991 a & b, Oliveira & Franklin 1993). The figure is slightly different at species level, with more than 15% of the primary forest species still absent from the secondary forest in our study. Actually, large taxonomic groups involve such a variety of different ecological forms that it is not surprising that one species at least may be able to recolonize rapidly the disturbed area. Inferring community structure or diversity from high taxa analysis might be therefore misleading and our opinion is that every effort should be made to associate limited species level analysis to large group analysis whenever possible.

2) Seasonality. Community structure descriptors are more variable and seasonal patterns of biodiversity more apparent in secondary forest, in parallel with larger humidity and temperature variations in the soils (Fig.7). The decrease in diversity during dry season contrast with the erratic patterns observed in the rainy season, and points to the importance of hydric factors even in the low seasonal climate of central Amazonia. Canopy was already nearly closed in the secondary forest, but the lower height of trees might have resulted in a thinner atmospheric buffer zone between the soil and the canopy, making superficial soil layers more sensible to climatic variations.

(3) Importance of generalist species. A group of seven parthenogenetic species of pantropical distribution represents a large part of the total number of Collembola collected in the studied area. Their relative abundance is globally much higher in the disturbed forest (59% of the total number of Collembola) than in primary forest (34 %) (Fig.6). The absolute number of specimens is also higher in secondary forest (1550 against 1174 for the 7 species together), except for *Isotomiella symetrimucronata*, in spite of the 24% decrease of the global number of Collembola: it is clear that the higher dominance of generalist species in secondary forest results both from an increase in their number (+32%) and from a dramatic decrease of the non-generalists (-52%). Whether autoecological processes are the prime determinant of these changes is open to debate. However, biotic factors may play an

important role as well, as the food web in the soil compartment was largely reorganized after disturbance. In particular, preliminary analyses have shown that the density of ants, which are probably the major predators of Collembola in lowland tropical soils, increased of 29% from primary to secondary forest, compared to the 24% reduction in the density of Collembola.

The high abundance of generalist species in secondary forest was an expected result. More puzzling in our study was the fact that these species were already present and largely dominant in the primary forest. The stability of the soil habitat in rainforests not disturbed by man could be therefore questioned, more especially as similar situations were found in several areas of Southeast Asia (unpublished data). Compared to temperate forest soils, the thinness and patchiness of the litter in many lowland tropical forest makes the superficial soil layers a potentially fragile habitat in spite of the protection ensured by several vegetation strata. This proneness to disturbance, be it by drought, excessive rain or changes in litter patchiness, may account in part for the observed high level of generalist species in primary forest. Greenslade and Greenslade (1980), working in Solomon islands, tentatively related the intriguing distribution of some of the generalist species cited here (*Isotomodes trisetosus* and *Isotomiella* probably *symetrimucronata*, identified as *minor* by the authors) to an opportunist behaviour in a situation of diffuse competition; their hypothesis may well hold for the primary forest soils cited here.

Six years after forest logging, the soil communities of Collembola had not yet recovered, in spite of highly favourable conditions, i.e. the small size of the disturbed plot, its inclusion in a large block of primary forest and a vigorous regeneration which has already led to a closed canopy forest. The productivity of the resources which sustain this fauna is not to incriminate, as shown by the levels of Collembola abundances in secondary forest, which stand over that of primary forest for several months<sup>5</sup>. The lower diversity of the vegetation in the secondary forest is unlikely to hinder the recovering of Collembola, which all have unspecialized trophic requirements in the studied communities. Two probably interrelated causes remain to explain the relatively low level of diversity:

- 1) a slow recolonization rate due to the low vagility of many species of Collembola and to the flat topography of the area which makes it unfavourable for passive dispersal;
- 2) long-term changes in the community structure, possibly linked to undetected modifications of abiotic parameters.

## Acknowledgements

We are grateful to Maria Lucia de Paula, Edson Palheta and Cláudio Sena for their help in the field and at laboratory. The work was funded by INPA Manaus and CNPq-Brasília. We thank an anonymous reviewer for his pertinent comments of the first draft.

## References

- Adis, J. and Schubart, H.O.R. 1984. Ecological research on arthropods in Central Amazonian forest ecosystems with recommendations for procedures. - In: Cooley, J. H. and Goley, F. B. (eds): Trends in ecological research for 1980s: 111-114. Nato, Conferences Serie I:Ecology Plenum Press, New York, London, 344pp.
- Betsch, J.-M. 1987. Effets des types d'aménagement de la forêt tropicale humide (Guyane française) sur les microarthropodes de la litière et du sol. Soil fauna and fertility. - Proc 9th Intern. Coll. Soil Zool. B. R. Striganova Ed., Moscow, Nauka, 183-191.
- Betsch, J.-M., Kilbertus, G., Couteaux, M. M. and Vannier, G. 1990. Microflore et faune du sol: indicateurs biologiques de la transformation de la forêt tropicale humide en agrosystème. - In: Mise en valeur de l'écosystème forestier Guyanais. 210-269.
- Bonnet, L., Cassagnau, P. and Deharveng, L., 1979. Recherche d'une méthodologie dans l'analyse de la rupture des équilibres biocénétiques: application aux Collembolés édaphiques des Pyrénées. Rev. Ecol. Biol. Sol, 16(3): 373-401.
- Chauvel, A. 1981. Contribuição para o estudo da evolução dos latossolos amarelos, distróficos, argilosos, na borda do platô na região de Manaus. Mecanismos de gibbsitização. - Acta Amazonica 11: 227-245.
- Connell, H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science, 199: 1302-1309.
- Dantas, M. 1978. Pastagens da Amazônia Central: ecologia e fauna do solo. - In: Inpa/Fua, Manaus, 95 pp. (Tese de Mestrado).

- Gama, M.M.da, Nogueira, A. and Murias Dos Santos, A.F.A. Effets du reboisement par *Eucalyptus globulus* sur les Collemboles édaphiques. Rev. Ecol. Biol. Sol, 28(1): 9-18.
- Gers, C. and Izarra, D. C. 1983. Rupture de l'équilibre biocénotique des populations de Collemboles à la station de ski de Calmazeille-Formiguères (Pyrénées Orientales). Bull. Soc. Hist. Nat., Toulouse, 119:63--69.
- Greenslade, P. and Greenslade, P.J.M. 1980. Relationships of some Isotomidae (Collembola) with habitat and other soil fauna. Proc. VII Int. Coll. Soil Zool.: 591-506
- Hüther, W. 1983 . Collembolen-Populationen brasilianischer Regenwalder und ihre Beeinflussung durch den Menschen. - Pedobiologia, 25: 317-323.
- Jordana, R., Arbea, J.I., Moraza, I., Montenegro, E., Mateo, M.D., Hernandez, M.A. and Herrera, L. 1987. Effect of reafforestation by conifers in natural biotopes of middle and South Navarra (Northern Spain). Revue Suisse Zool., 94(3): 491-502.
- Magurran, A. E. 1988. Ecological diversity and its measurement. - Croom Helm ed., London. 179 pp.
- Melo, L. A. S. 1985 . Impacto do manejo de agrossistemas sobre a mesofauna do solo em áreas de terra firme, na região de Manaus. - In Inpa/Fua, 117 pp. (Tese de Mestrado).
- Oliveira, E. P. 1983 . Colêmbolos (Insecta, Collembola) epigêicos como indicadores ecológicos de ambientes florestais. - In: Inpa/Fua, 104 pp. (Tese de Mestrado).
- Oliveira, E.P. and Franklin, E. 1993. Efeito do fogo sobre a mesafauna do solo: recolonização em áreas queimadas. Pesq. agropec. bras., Brasília, 28 (3): 357-369.
- Ribeiro, E. F 1986 . Oribatideos (Acari: Oribatida) colonizadores de folhas em decomposição sobre o solo de três áreas florestais da Amazônia Central. - In: Inpa/Fua, 178pp. (Tese de Mestrado).
- Ribeiro, M. N. G. and Adis, J. 1984 . Local rainfall variability - a potencial bias for bioecological studies in Central Amazon. - Acta Amazonica, 14: 159-174.

- Silva del Pozo, X. and Blandin, P. 1991a. Les Macroarthropodes édaphiques d'une forêt mésothermique primaire de l'Équateur occidental: abondances saisonnières et distribution spatiale. - Rev. Ecol. Biol. Sol, 28 (4): 421-433.
- Silva del Pozo, X. and Blandin, P. 1991b .Les peuplements de Macroarthropods édaphiques à différentes étapes de la reconstitution de la forêt mésothermique en Équateur occidental. - Rev. Ecol. Biol. Sol, 28 (4): 435-442.
- Takeda, H.. 1981. Effects of shifting cultivation on the soil meso-fauna with special reference to Collembola populations in the north-east Thailand. Memoirs of the College of Agriculture, Kyoto University, n° 118, series n° 5:45-60.
- Teixeira, L. B. and Schubart, H. O. R. 1988 . Mesofauna do solo em áreas de floresta e pastagem na Amazônia Central. - Boletim de Pesquisa n° 95, 16pp.
- Usher M.B., 1988. Soil invertebrates: a review of species, populations, communities, modelling and conservations with special reference to the African Continent. J. Afri. Zool. 102: 285-300.